



MORPHOLOGY OF A SPECIMEN OF *SUPERSAURUS* (DINOSAURIA, SAUROPODA) FROM THE MORRISON FORMATION OF WYOMING, AND A RE-EVALUATION OF DIPLODOCID PHYLOGENY ¹

(With 15 figures)

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ABSTRACT: A new specimen of *Supersaurus vivianae* is described, providing additional information about the osteology of *Supersaurus*. The single *Supersaurus* individual that the WDC quarry produced allows a re-examination of elements referred to *Supersaurus* from the Dry Mesa quarry. The osteology supports maintaining the generic distinction of *Supersaurus*. Phylogenetic evaluation finds a monophyletic Apatosaurinae containing [*Apatosaurus* + *Supersaurus*] + *Suuwassea*, and a monophyletic Diplodocinae containing [*Diplodocus* + *Seismosaurus*] + *Barosaurus*, although the generic distinction of *Seismosaurus* is not supported in the current analysis.

Key words: Dinosauria. Sauropoda. *Supersaurus*. Phylogeny. Morrison Formation.

RESUMO: Morfologia de um espécime de *Supersaurus* (Dinosauria, Sauropoda) da Formação Morrison de Wyoming e uma reavaliação da filogenia de diplodocídeos.

Um novo espécime de *Supersaurus vivianae* é descrito, acrescentando informações sobre a osteologia de *Supersaurus*. O único indivíduo de *Supersaurus* coletado no afloramento WDC permite o re-exame dos elementos referidos a *Supersaurus* do afloramento de Dry Mesa. A osteologia suporta a manutenção da distinção genérica de *Supersaurus*. Uma avaliação filogenética resultou em um grupo monofilético Apatosaurinae contendo [*Apatosaurus* + *Supersaurus*] + *Suuwassea*, e um grupo monofilético Diplodocinae contendo [*Diplodocus* + *Seismosaurus*] + *Barosaurus*, embora a distinção genérica de *Seismosaurus* não esteja suportada na presente análise.

Palavras-chave: Dinosauria. Sauropoda. *Supersaurus*. Filogenia. Formação Morrison.

INTRODUCTION

Diplodocoid taxa rank among the earliest described and best-known sauropods (MARSH, 1896; HATCHER, 1901; HOLLAND, 1906; LULL, 1919; GILMORE, 1936), with new taxa continuing to be described, such as *Suuwassea* (HARRIS & DODSON, 2004) and *Dinheirosaurus* (BONAPARTE & MATEUS, 1999). Recent studies have provided needed attention to diplodocoid phylogenetic systematics (UPCHURCH *et al.*, 2004; TAYLOR & NAISH, 2005; MCINTOSH, 2005; HARRIS, 2006), yet several diplodocid taxa have remained problematic due to their fragmentary nature, notably *Seismosaurus* and *Supersaurus*.

In 1985, J.A. Jensen erected three sauropod genera based on material collected from Dry Mesa Quarry:

Ultrasauros macintoshi; *Dystylosaurus edwini*; and *Supersaurus vivianae*. All three have had complex nomenclatural histories (*e.g.*, JENSEN, 1987; CURTICE, 1995; CURTICE *et al.*, 1996; CURTICE & STADTMAN, 2001), with the types of both *Ultrasauros* and *Dystylosaurus* eventually sunk into *Supersaurus vivianae* (CURTICE, 1995; CURTICE & STADTMAN, 2001). In addition, some of the specimen numbers have changed in the last two decades.

The name *Supersaurus* was erected for a single scapulocoracoid, BYU 12962 (JENSEN, 1985). Dozens of elements have been referred to this taxon since. Some referrals, such as the matching right scapulocoracoid, are unambiguous. Other elements have been referred based on quarry location, relative size, and hypotheses of phylogenetic

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position. The depositional circumstances and multiple disarticulated sauropod taxa in the Dry Mesa quarry made unambiguous referrals of other elements difficult. As a result, *Supersaurus* has largely been excluded from phylogenetic analyses, and opinion on its generic validity has been mixed. At one time J.S. McIntosh thought *S. vivianae* was a large species of *Barosaurus*, but more recently supported generic distinction (McINTOSH, 2005; GLUT, 1997). Alternately, it has been suggested that *Supersaurus* should be synonymized with *Seismosaurus*, or that the genus is a *nomen dubium* (GILLETTE, 1994).

A second specimen, a single individual from a quarry in Wyoming, makes it possible to evaluate the taxonomic status of referred supersaur skeletal elements in the BYU collection. Combined with morphological data from WDC DMJ-021 it is now possible to provide an emended diagnosis of the species, and to add *Supersaurus* to existing phylogenetic analyses. Approximately 30% of the skeleton has been recovered of WDC DMJ-021 which combined with the BYU specimen yields knowledge of 45-50% of the osteology of *Supersaurus*.

MATERIAL AND METHODS

Abbreviations: Institutional. AMNH, American Museum of Natural History, New York, New York; BYU, Brigham Young University, Provo, Utah; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; DMJ, Douglas Morrison Jimbo site; DMNH, Denver Museum of Nature and Science, Denver, Colorado; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico; NSMT, National Science Museum, Tokyo, Japan; UWGM, University of Wyoming Geological Museum, Laramie, Wyoming; WDC, Wyoming Dinosaur Center, Thermopolis, Wyoming; YPM, Yale Peabody Museum, New Haven, Connecticut.

MATERIAL

A single individual (WDC DMJ-021) with approximately 30% of the skeleton was discovered in the Morrison Formation near Douglas Wyoming. The specimen includes a relatively complete presacral column, sacral fragments, and incomplete caudal series. Remains of costal elements, fragmentary pelvic and femur, and

complete tibiae and fibulae were also recovered. Elements previously referred to this taxon were also analysed. We follow CURTICE *et al.* (1996) in using current BYU specimen numbers, with original numbers noted when necessary for continuity with earlier publications (Tab. 1).

A phylogenetic analysis was conducted using a modified version of HARRIS & DODSON's (2004) data matrix. The data set was modified by the addition of *Supersaurus* and *Seismosaurus* (see Appendix 1 for character scoring), as well as four new characters (Appendix 2), in part in an attempt to distinguish *Seismosaurus* from *Diplodocus*.

TAPHONOMY

WDC DMJ-021 was found in the Morrison Formation near Douglas Wyoming (Fig.1). Taphonomy of the Jimbo Quarry is interpreted as a debris-flow deposit that buried a single sauropod skeleton (LOVELACE *et al.*, 2003, LOVELACE, 2004; LOVELACE, 2006). While allocthanous in nature, the debris flow appears to have preserved an autocthanous burial of the specimen, prior to the mass wasting event (LOVELACE, 2006). The taphonomic interpretation of a single individual is backed up by relative size of preserved elements, and the absence of duplicate elements.

SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1887
SAUROPODA Marsh, 1878
DIPLODOCIDAE Marsh, 1884
APATOSAURINAE Janensch, 1929
Supersaurus vivianae Jensen, 1985

Holotype – BYU 12962 JENSEN (1985), a large diplodocid left scapulocoracoid.

Referred specimens – BYU 4839, BYU 9024, BYU 9044, BYU 9045, BYU 9085, BYU 10612, BYU 12424, BYU 12555, BYU 12639, BYU 12819, BYU 12861, BYU 12946, BYU 12962, BYU 13016, BYU 13018, BYU 13981, BYU 16679, BYU 17462; Dry Mesa specimens likely pertaining to the type individual. Remains include a nearly complete pelvic girdle and sacrum, a right scapulocoracoid, several axial elements from the cervical, dorsal, and caudal region (see Tab.1 for element identification). WDC DMJ-021, a single associated specimen including a relatively complete presacral column

(portions of 10 cervical vertebrae and 5 dorsal vertebrae), sacral fragments, and representative but incomplete caudal series. Several costal elements, fragmentary pelvic and femoral remains, and

complete tibiae and fibulae. While a scapula is not known for WDC DMJ-021, other elements are identical to axial elements referred to the type individual of *Supersaurus*.

TABLE 1. Status of Dry Mesa Quarry specimens referred to *Supersaurus*. “Specimen #” column reflects current BYU ascension numbers; “Element” column provides a brief description of element; “Interpreted Referral Status” column provides current status on taxonomic referral.

SPECIMEN #	ELEMENT	INTERPRETED REFERRAL STATUS
BYU 9025 ¹	left scapulocoracoid; (holotype)	N/A
BYU 12962 ¹	right scapulocoracoid	Yes; mate to BYU 9025
BYU 12946 ¹	right ischium	Yes; verified by WDC DMJ-021
BYU 12854 ⁶	distal proximal caudal	No; reassigned in this paper to Diplodocinae
BYU 12843 ^{1,5}	distal proximal caudal	No; reassigned in this paper to Diplodocinae
BYU 9084 ¹	12 articulated mid-caudals	No; reassigned in this paper to Diplodocinae
BYU 9077 ¹	mid-caudal vertebra	No; reassigned in this paper to Diplodocinae
BYU 9024 ²	mid-cervical vertebra	Yes; verified by WDC DMJ-021
BYU 9045 ^{3,5}	proximal caudal vertebra	Yes; verified by WDC DMJ-021
BYU 9044 ^{3,4}	posterior dorsal vertebra	Yes; verified by WDC DMJ-021
BYU 12390 ⁵	Carpal	Indeterminate
BYU 9000 ⁵	Phalanx	Indeterminate
BYU 13744 ⁵	left ulna	No; 20-25% larger than predicted by length of tibia for WDC DMJ-021
BYU 12555 ⁵	left ischium	Yes; mate to BYU 12946
BYU 12424 ⁵	right pubis	Yes; verified by WDC DMJ-021
BYU 4839 ⁵	caudal vertebra	Fragmentary; CURTICE (1996) suggests it is
BYU 12639 ⁵	caudal vertebra	Yes; not verified by WDC DMJ-021
BYU 12819 ⁵	caudal vertebra	Yes; verified by WDC DMJ-021
BYU 12814 ⁵	dorsal vertebra	Unable to confirm
BYU 9192	caudal vertebra	Unable to confirm
BYU 13018 ⁵	pelvis (left ilium/four sacral vertebra)	Yes; not verified by WDC DMJ-021
BYU 13981	mid caudal vertebra	Referred to <i>Supersaurus</i> in the text
BYU 13016	mid caudal vertebra	Referred to <i>Supersaurus</i> in the text
BYU 12861	mid caudal vertebra	Referred to <i>Supersaurus</i> in the text
BYU 10612	mid caudal vertebra	Referred to <i>Supersaurus</i> in the text
BYU 9085	mid caudal vertebra	Referred to <i>Supersaurus</i> in the text
BYU 17462	anterior caudal vertebra	Referred to <i>Supersaurus</i> in the text
BYU 4503 ⁵	dorsal vertebra	Yes; verified by WDC DMJ-021
BYU 16679	caudal vertebra	Referred to <i>Supersaurus</i> in the text

(¹ JENSEN, 1985; ² JENSEN, 1987; ³ CURTICE & CURTICE, 1996; ⁴ CURTICE *et al.*, 1996; ⁵ CURTICE & STADTMAN, 2001) – ⁶CURTICE, 1996.

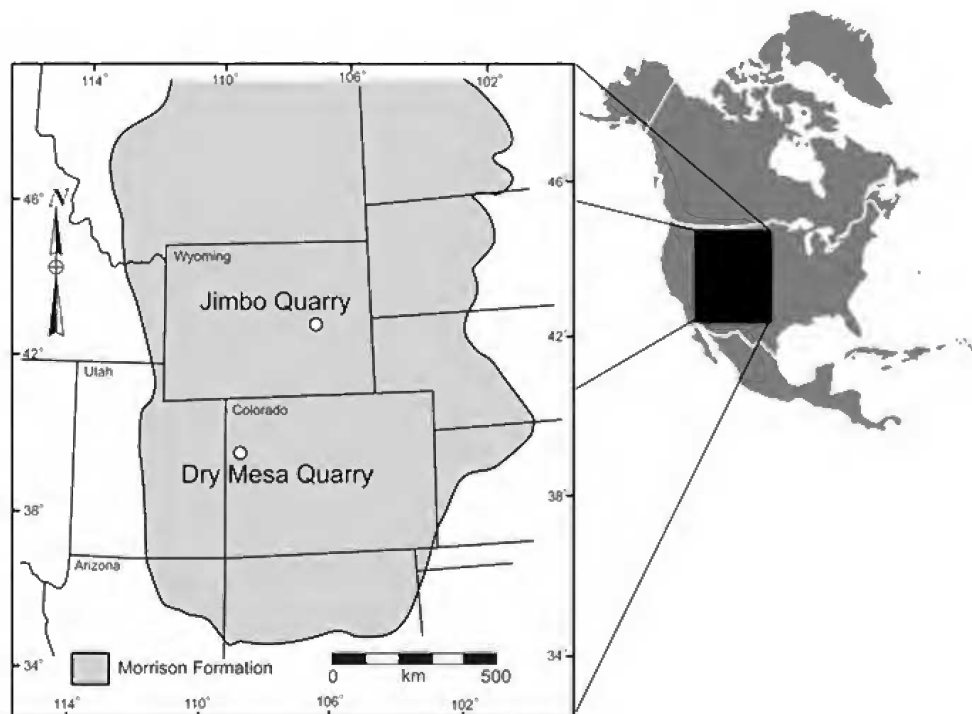


Fig.1- The range of Morrison Formation (shaded) exposed throughout the Rocky Mountain region of western North America. Modified after DUNAGAN & TURNER (2004).

Referral of all material is supported by relative position within their respective quarries (CURTICE & STADTMAN, 2001; LOVELACE, 2006), size of the skeletal elements, and congruence of phylogenetically significant diplodocid characters between the scapula and referred material (see below).

Emended Diagnosis – Large diplodocid sauropod with the following characteristics: elongate cervical vertebrae (elongation index ranging from 4-7) with an extreme narrowing of the ventral surface of the vertebral body at midlength; well-developed parallel keels on the ventral surface of the cervical series; small ventral pleurocoel located between the parapophyses with dual pneumatopores divided by an anterior-posteriorly directed septa; lateral pleurocoels simple, shallow depressions with small pneumatopores; posterior dorsals with proportionately tall neural spines (> than 0.5 of vertebral height) and reduced neural arch height; anterior dorsals with dorsal vertebral bodies with moderate midline keel and shallow lateral sulci; posterior dorsals opisthocelous; anterior caudal vertebrae with prominent ventral keel, and shallow pleurocoels; ribs pneumatized, with anterior-posteriorly expanded shafts; scapular blade expanded dorsally; deltoid ridge perpendicular to the acromian ridge.

RESULTS AND DISCUSSION

DESCRIPTION OF THE MATERIAL

Cervical vertebrae – The cervical vertebrae of *S. vivianae* are extremely elongate (length of centra for BYU 9024 is 1380mm). Centra length exceeds even those of *Sauroposeidon*, which was reported as having the longest cervical vertebrae of any known sauropod (WEDEL *et al.*, 2000); the greatest centra measurement of *Sauroposeidon* is 1250mm. While no cervical vertebra is complete, preserved elements are adequate for description and comparison. Supersaur cervical vertebral autapomorphies include a mediolaterally narrow ventral surface (5-8cm) of the middle centra. Cervical vertebrae lack elaborate pneumatic fossae (pleurocoels), a feature noted by JENSEN (1985) as differing greatly from the condition typically seen in the Diplodocidae. Cervical ribs are sub-equal in length to their respective centra, with some extending slightly beyond the posterior limit of the cotyle.

A mid-cervical vertebra (BYU 9024; Fig.2) originally assigned to *Ultrasauros* (JENSEN, 1985) was later referred to the type individual by JENSEN (1987). BYU 9024 compares favorably to preserved WDC cervical vertebrae, supporting its referral to the type

individual. The WDC specimen includes substantial portions of ten cervical vertebrae, representing most of the cervical column. Seven of the cervical vertebrae contain nearly complete centra, each over a meter in length.

In cross section the form of the centra can be generalized as an I-beam (Fig.3E). The diameter of pneumatopores on the lateral surface of the centra are no more than 30-80mm. This condition is reduced in comparison to the pneumatopores in several *Apatosaurus*, and contrasts greatly with the elaborate pneumatic structures seen in the centra of *Diplodocus* and *Barosaurus* (Fig.3). On the ventral surface just posterior of the centroparapophyseal lamina there are two pneumatopores separated by a medial septum. This feature appears in all cervicals where this area is preserved (both anterior and posterior cervical vertebrae demonstrate this condition). Figure 4 shows this condition in cervical vertebrae (Cv.) 14 of *Apatosaurus ajax* as well as in Cv.13 of *Supersaurus*; however this feature is absent in *Barosaurus* (LULL, 1919) and *Diplodocus*. More work is needed to determine the distribution of this character in diplodocids.

Dorsal vertebrae – Five dorsal vertebrae have been recovered for WDC DMJ-021; four vertebrae preserve complete centra, one lacks only the transverse processes, while two preserve isolated neural spines. BYU 9044 exhibits features seen in several of WDC dorsal vertebrae, supporting CURTICE

et al.'s (1996) referral to the same individual as the type. WDC dorsal vertebra WDC DMJ-021-085 is extremely similar to mid-anterior dorsal vertebrae BYU 4503 (approximately number 4; CURTICE & STADTMAN, 2001), supporting BYU 4503's referral to the Dry Mesa *Supersaurus*.

Supersaurus dorsal vertebrae demonstrate several synapomorphic characters with *Apatosaurus*. The neural spines (measured from the junction between postzygapophyses to the top of the neural spine) of the posterior dorsal vertebrae make up more than half the height of the vertebra. This is similar to the condition seen in *Apatosaurus*. Both *Diplodocus* and *Barosaurus* exhibit posterior dorsal neural spine heights that contribute to less than half of the entire vertebrae (Fig.5). The bifid neural spines are lost prior to dorsal seven, and possibly as early as dorsal four or five (inferred from the merging of the spinoprezygapophyseal laminae with the prespinal lamina), unlike in *Diplodocus*. The cleft in the posterior dorsal neural spines of *Diplodocus* is absent in *Supersaurus*.

Preserved dorsal centra of *Supersaurus* exhibit a ventral keel on the centra, as observed in *Apatosaurus* (UWGM 15556). While the posterior dorsal vertebrae of all other diplodocids are amphiplatean (GILMORE, 1936; HATCHER, 1901; LULL, 1919), the posterior dorsals of both *Supersaurus* specimens are opisthocelous, a probable autapomorphy of *Supersaurus*.

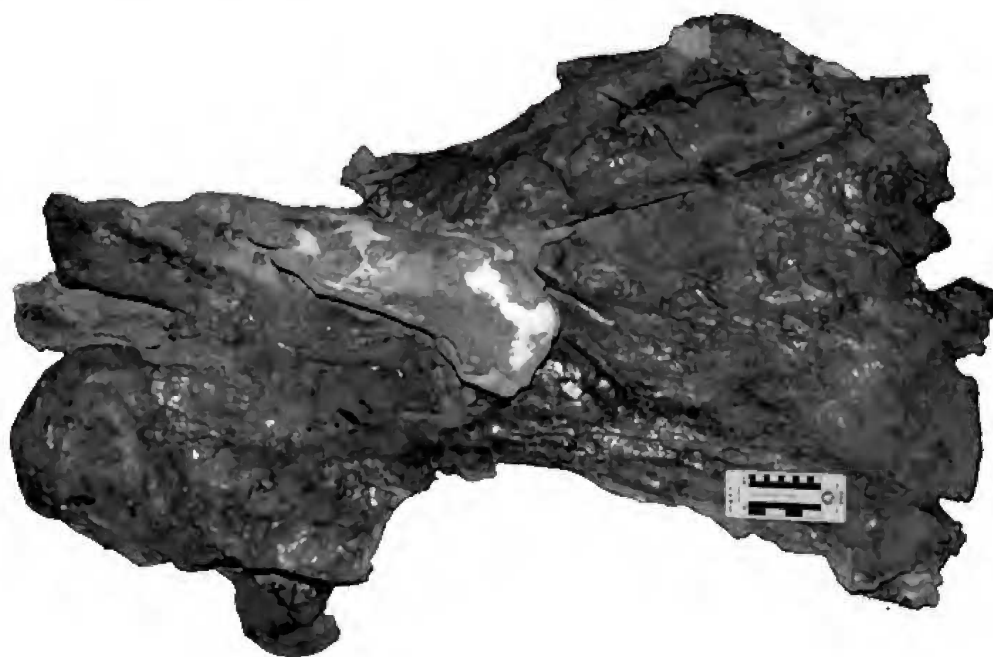


Fig.2- Cervical vertebrae 11 or 12, referred to type specimen of *Supersaurus vivianae* (BYU 9024).

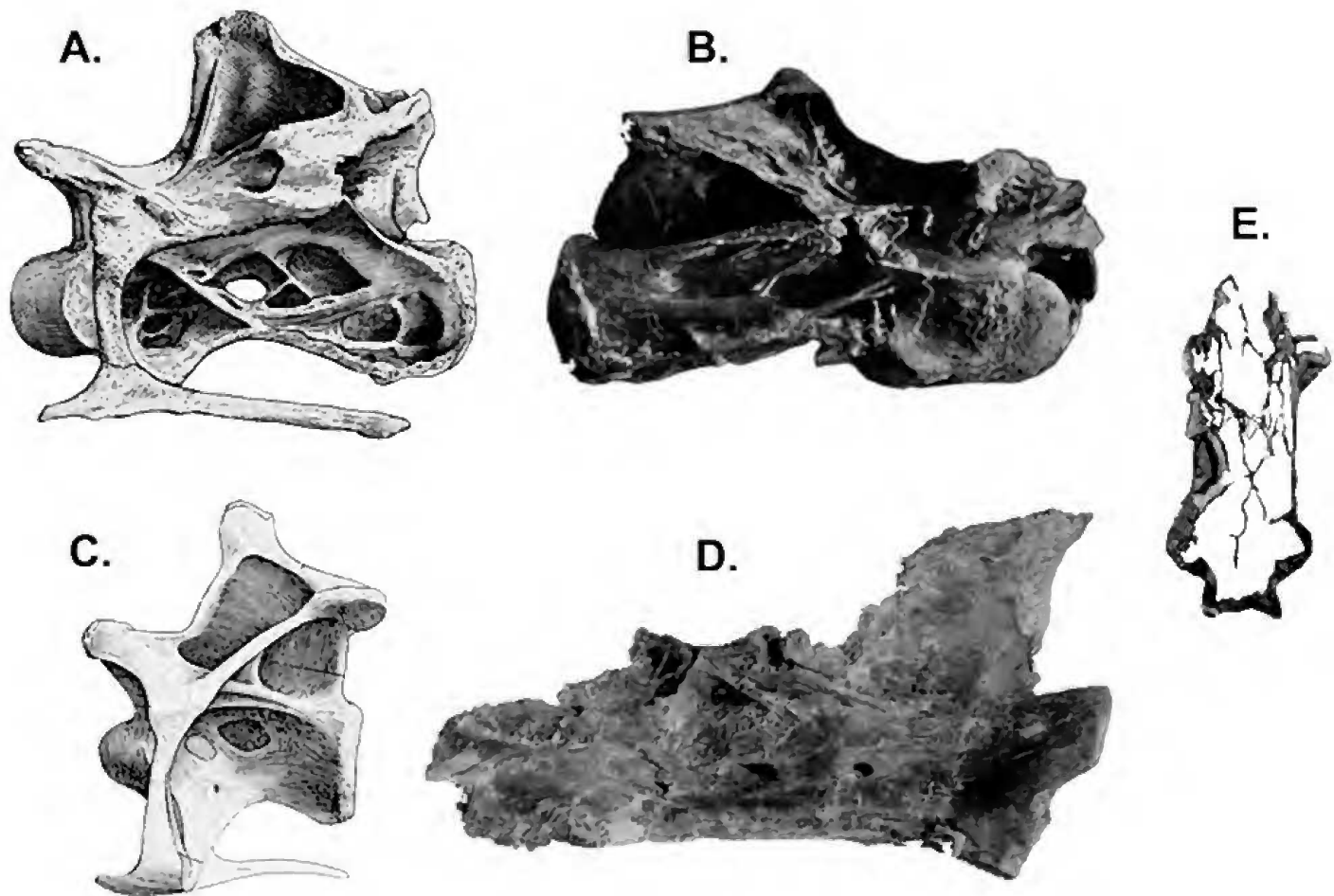


Fig.3- Lateral views of cervical vertebrae from A, *Diplodocus carnegii* (HATCHER, 1901); B, *Barosaurus lentus* (LULL, 1919); C, *Apatosaurus louisae* (GILMORE, 1936); D and E, *Supersaurus vivianae*; demonstrating pneumatic modifications of centra. *Supersaurus* has the least amount of modification with minimal size for pneumatopores. Internal structure is similar to that seen in other diplodocids (JANENSCH, 1947). Left lateral view of Cv.13 (D, missing the condyle, prezygapophyses and neural spine; length of incomplete centra 94cm). E, cross section through Cv.11, 5cm posterior of the diapophysis.

Caudal vertebrae – CURTICE (1996) and MACINTOSH (2005) suggest that diplodocid caudal vertebrae are a useful source of taxonomically significant characters. *Supersaurus* caudals share the presence of pneumatic fossae with *Barosaurus* and *Diplodocus*. Aside from this character, they exhibit numerous apatosaurine synapomorphies. Relative to diplodocines the anterior caudal vertebrae have short (less than twice the height of the centra) and distally expanded (rectangular box-like) neural spines (Fig.6) that lack a bifid cleft. The centra are heart-shaped in cross-section, have well-developed anterior cotyles and a platyeon posterior surface, contrary to the condition reported by CURTICE (1995) in which caudal vertebrae are reported as having a pronounced posterior ball. Inspection shows neither BYU 9045 nor WDC DMJ-021-083 exhibit

a pronounced posterior ball, nor do any other caudals from either locality. We were unable to confirm the presence of a hyposphene/hypantrium complex on any of the BYU *Supersaurus* caudals, nor is one present on WDC DMJ-021.

Anterior caudal vertebrae centra exhibit a prominent ventral midline keel, as seen in *Apatosaurus excelsus* (GILMORE, 1936). The keel disappears by caudal vertebrae 12 or 13. Centra length is subequal over the first 30 caudal vertebrae, as in *Apatosaurus*. The height of the caudal neural spines decreases rapidly from anterior to posterior, a condition seen in both *Apatosaurus* and *Barosaurus*, but unlike the very slight decrease in anterior to posterior neural spine height seen in *Diplodocus* and *Seismosaurus* (see Figs.7-8).

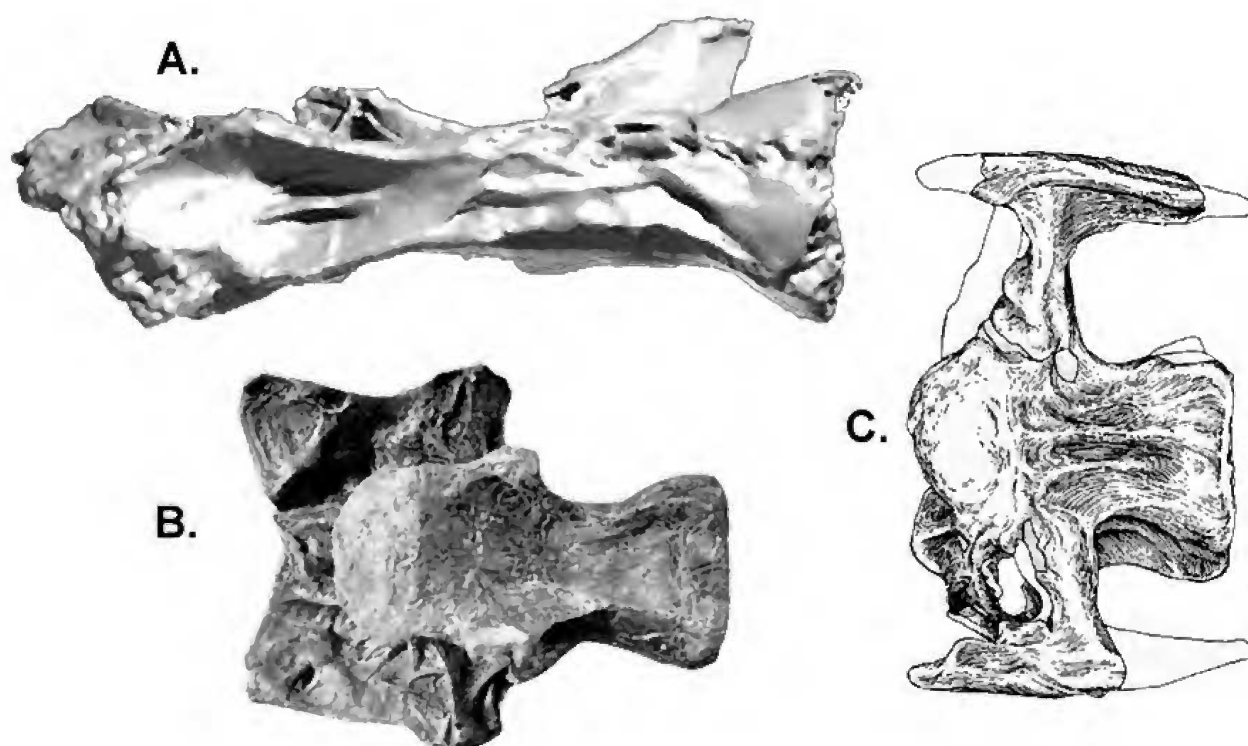


Fig.4- Ventral views of posterior cervical centra from A, *Supersaurus*; B, *Barosaurus lentus* (LULL, 1919); and C, *Apatosaurus ajax* (UPCHURCH *et al.*, 2004). There are two pneumatopores along the midline of the centra slightly posterior to the parapophyses, each pair separated by a sagittal septum. This condition is seen in *A. ajax* as well as *Supersaurus*, but not observed in *Barosaurus* (LULL, 1919) or DMNH 1494 *Diplodocus*.

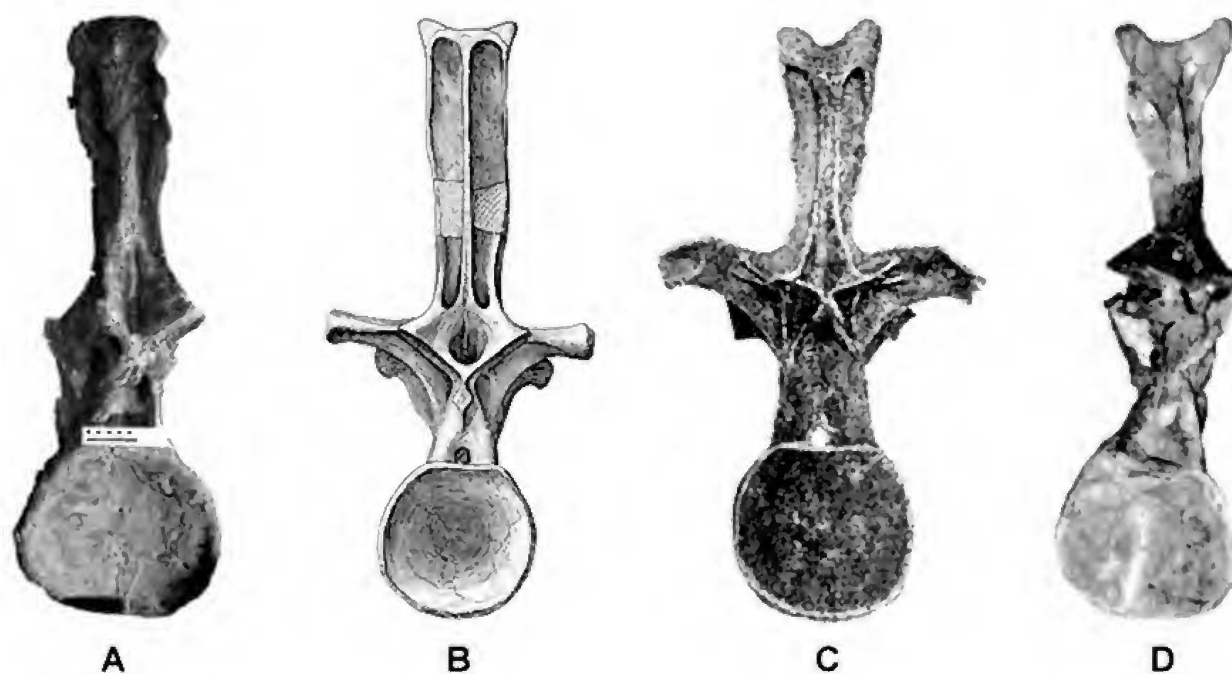


Fig.5- Dorsal vertebrae (third pre-sacral for each species) scaled to the same height to demonstrate relative position of the hyposphene on posterior dorsals. A, *Supersaurus* (WDC DMJ-021); B, *Apatosaurus louisae* (GILMORE, 1936); C, *Diplodocus* (HATCHER, 1901); D, *Barosaurus* (LULL, 1919). The ratios (relative height of centra and neural arch to the height of the neural spine) are 0.44, 0.40, 0.53, and 0.52 respectively, showing that diplodocines have a taller neural arch relative to *Supersaurus* and *Apatosaurus*.

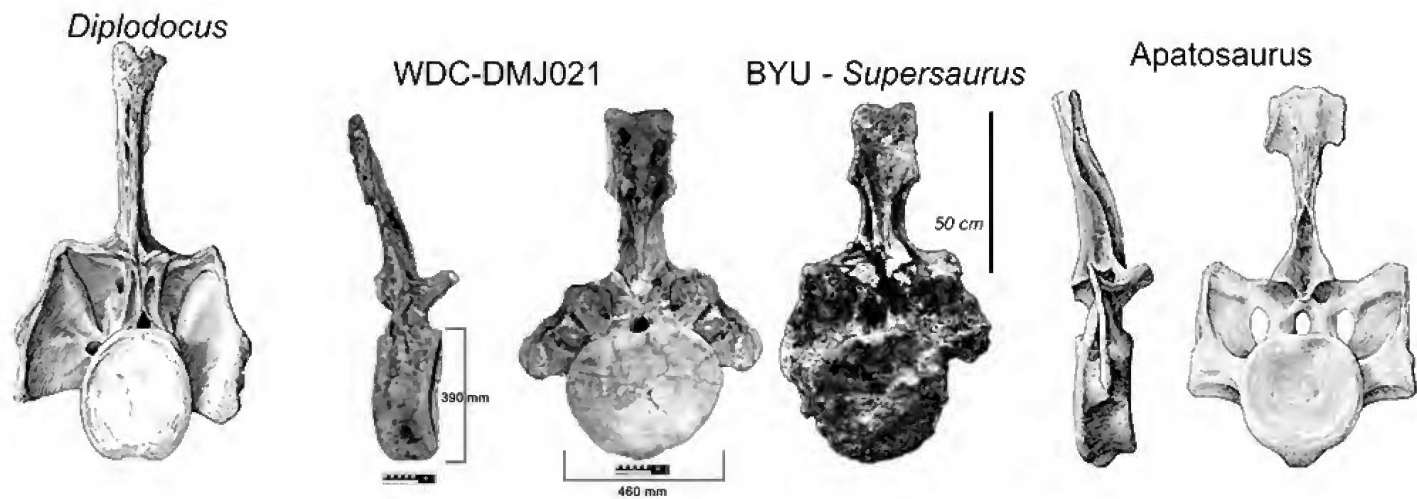


Fig.6- Caudal vertebrae of *Diplodocus*, *Supersaurus*, and *Apatosaurus* shown to demonstrate differences in the height of the neural spine relative to the centra. Note also the distally expanded neural spines of both *Supersaurus* and *Apatosaurus*; in lateral view the keel is apparent as well.

The caudal vertebrae of *S. vivianae* are easily distinguishable from the caudal vertebrae of *Diplodocus* or *Barosaurus*. None of the WDC caudal vertebrae demonstrate the classic diplodocine ventral longitudinal hollow. Nor do the anterior caudal vertebrae exhibit tall and narrow neural spines with a deep cleft at the distal end, as in *Diplodocus* and *Seismosaurus*.

We evaluated these characters in referred caudal material in the BYU collections (Table 1). BYU 12854, 12843, 9084 (12 articulated mid caudal vertebrae), and 9077 are incompatible with the vertebrae found at the WDC site, and should be reassigned to *Diplodocinae incertae sedis* based on their well-developed ventral longitudinal hollow.

Based on size and morphological similarity with WDC DMJ-021, BYU caudal vertebrae 12639, 13981, 13016, 12861, 10612, 9085, 17462, and 16679 can be confidently assigned to the type individual of *Supersaurus vivianae*.

Ribs – MARSH (1896) figured pneumatic cavities from a costal element of *A. excelsus*, and GILMORE (1936) published an image and description of a pneumatic cavity in a dorsal rib of *A. louisae* (Fig.9). *Supersaurus* provides unambiguous evidence of pneumatized ribs (LOVELACE *et al.*, 2003). If MARSH (1896) and GILMORE (1936) are correct, then this condition may be synapomorphic to apatosaurines. Alternately,

amongst diplodocids pneumatic ribs may be an apomorphic condition of *Supersaurus*.

The length of the longest preserved rib is 305cm. Even on an animal as large as *Supersaurus* this is relatively long. This results in a deep thoracic cavity (Fig.7). This is at odds with *Barosaurus* and *Diplodocus*, but similar to *Apatosaurus* (Figs.7-8). The robust, laterally expansive distal portions of the ribs are more similar to *Apatosaurus* (GILMORE, 1936) than to diplodocines, even in large diplodocine taxa like *Seismosaurus*.

Pectoral girdle – The only known pectoral elements for *Supersaurus* are the scapulocoracoids from Dry Mesa (Fig.10). Scapulocoracoid BYU 9025 demonstrates a deltoid ridge that is perpendicular to the acromian ridge and the scapular blade is one-half the entire length of the scapulocoracoid. Both of these features are seen in *Apatosaurus* but not in *Diplodocus* or *Barosaurus*, which have relatively short scapular blades, and an acute angle between the deltoid ridge and the acromian ridge. This angle is much stronger in *Barosaurus* than it is in *Diplodocus*. The apatosaurine nature of the scapulocoracoids further reinforces the referral of BYU elements to the type scapula, as well as our referral of WDC DMJ-021 to *Supersaurus*.

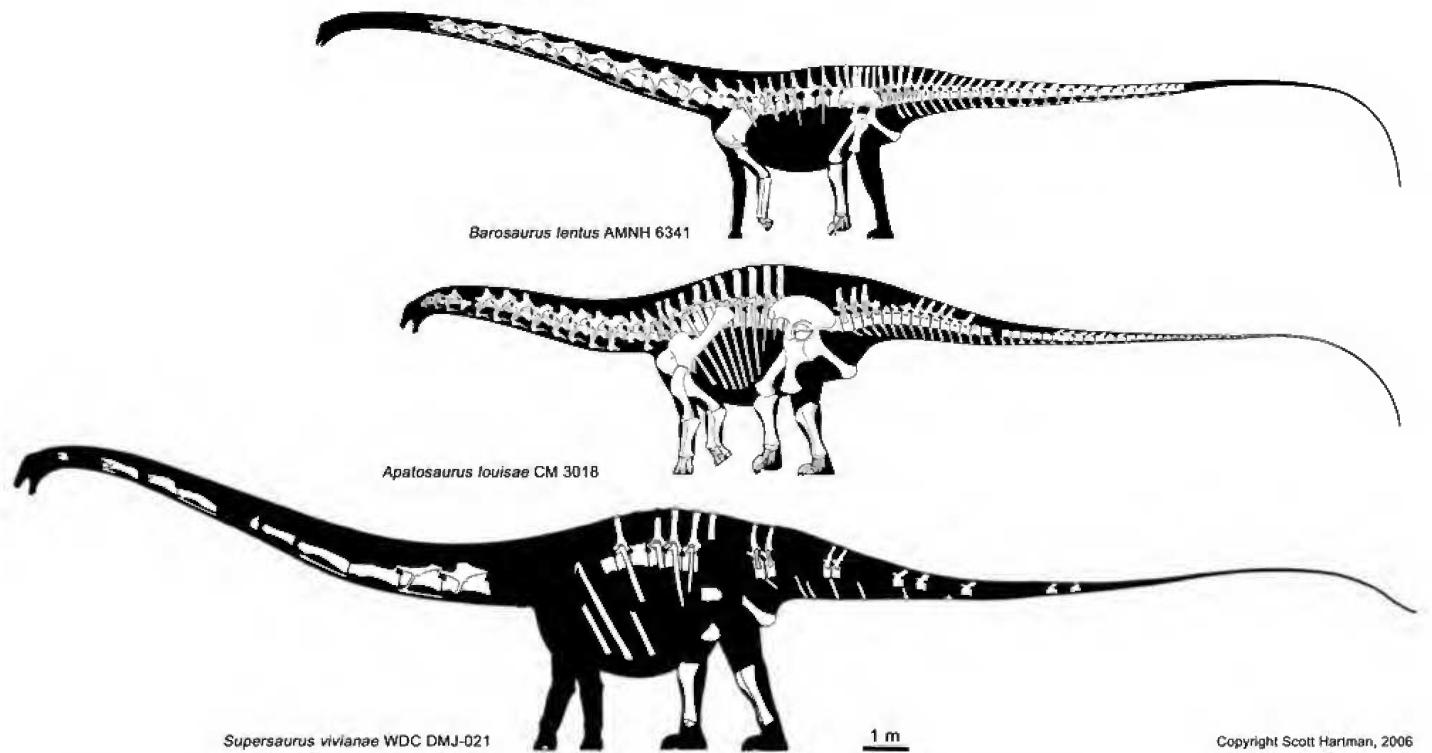


Fig.7- Comparative skeletal reconstructions of *Barosaurus lentus*, *Apatosaurus louisae*, and *Supersaurus vivianae* to the same scale.

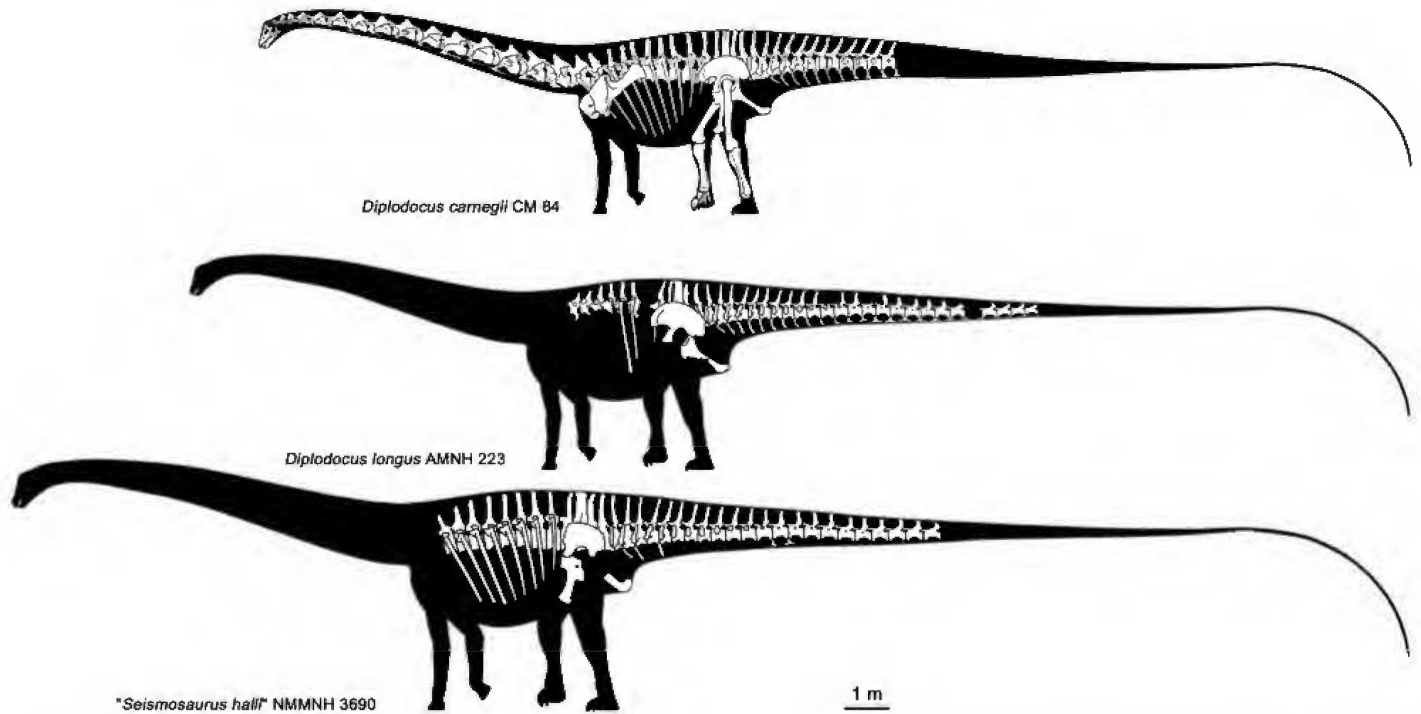


Fig.8- Comparative skeletal reconstruction of *Diplodocus carnegii*, *D. longus*, and NMMNH 3690, "*Seismosaurus*", to the same scale.

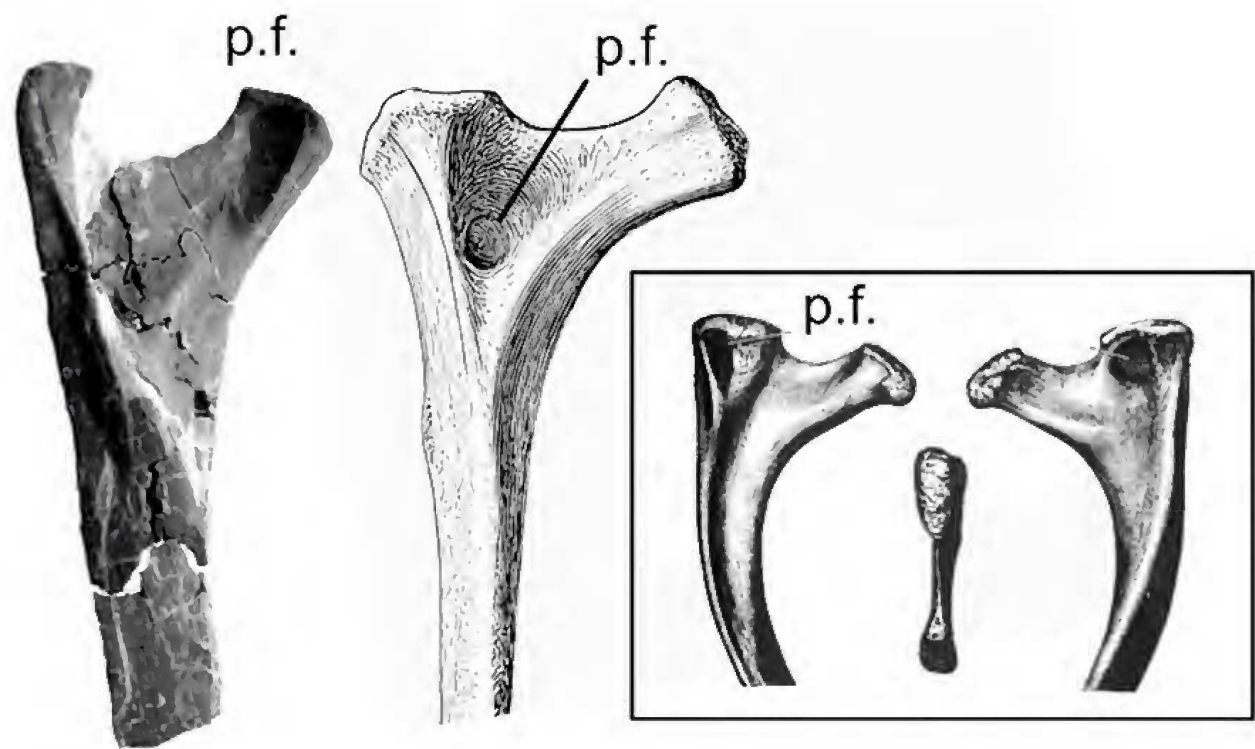


Fig.9- Pneumatic ribs described from the apatosaurines: A, *Supersaurus* (LOVELACE *et al.*, 2003); B, *Apatosaurus louisae* (GILMORE, 1936); and C, *Apatosaurus excelsus* (MARSH, 1896). p.f. = pneumatic foramen

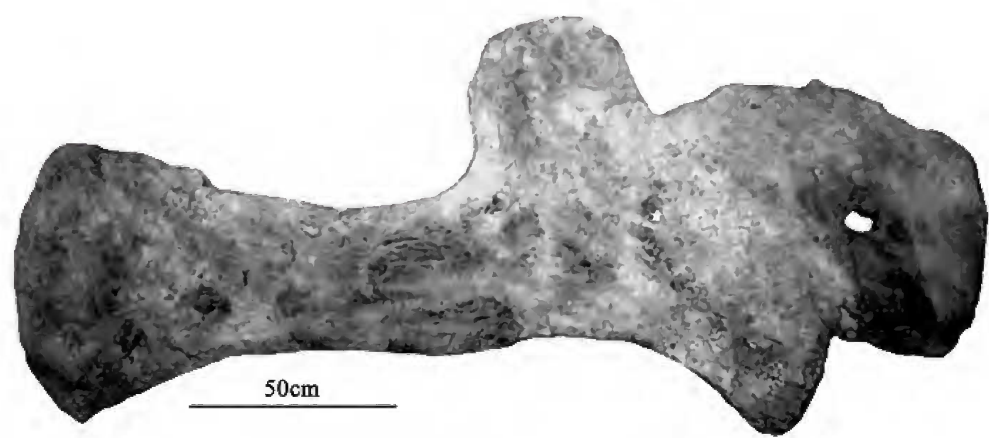


Fig.10- Lateral view of *Supersaurus* right scapulacoracoid (BYU 9025).

Forelimbs – Because *Barosaurus* forelimbs are poorly described, data from *Apatosaurus* and *Diplodocus* (a good proxy for *Barosaurus* limb elements; McINTOSH, 2005) are used as a model for diplodocid proportions; expected ratios were used for estimating lengths for missing *Supersaurus* limb elements. Using these predicted ranges, we can safely conclude no additional *Supersaurus* forelimb elements were recovered from the Dry Mesa Quarry. The ulna (BYU

13744) referred to the type specimen of *Supersaurus* (CURTICE & STADTMAN, 2001) measures 1280mm, while the maximum predicted value (relative to the scapula) for the ulna is 1012mm, a 20% discrepancy. Therefore the referral of BYU 13744 to *Supersaurus* cannot be supported.

No humerus was located in the BYU collection that matched the predicted range of humeral lengths. BYU 17386 has been informally referred to

Supersaurus. Using the same methods as above, a predicted range was generated. The length of BYU 17386 is 1710mm, while the maximum predicted value was 1424mm, a 17% discrepancy.

Pelvic girdle – CURTICE & STADTMAN (2001) referred an articulated sacrum and right ilium (BYU 13018), a left ischium (BYU 12555), and a right pubis (BYU 12424) to *Supersaurus*. The pelvis demonstrates dorsoventral shearing that depressed the right ilium ventrally and elevated the left sacral ribs dorsally relative to the midline of the sacral centra (Fig.11).

The ischium appears to be the match to the element referred previously by JENSEN (1985), whose referral was supported by CURTICE & STADTMAN (2001). A partial ischium preserved with WDC DMJ-021 is identical to both BYU ischia, supporting referral of these specimens to *Supersaurus*. Likewise, a pubic boot and partial shaft of the left pubis (WDC DMJ-021-233) is represented in the WDC specimen. The boot is very similar to that preserved in the BYU pubis, consistent with previous referrals (Fig.12).

Comparisons of the ilium, pubes and ischia with other diplodocids reveal additional apatosaurine affinities, including a short, robust pubic

peduncle of the ilium, and a large and fully enclosed obturator foramen. In particular, the robust margin surrounding the obturator foramen contrasts with the condition in *Barosaurus*, which is not completely enclosed (McINTOSH, 2005). *Supersaurus* and *Apatosaurus* also share a large distal expansion of the ischia (McINTOSH, 1990).

Hind limbs – The tibiae and fibulae of both limbs are present in the WDC specimen. Tibiae are deformed, but exhibit an intermediate level of robusticity, in between that of *Apatosaurus* and *Diplodocus*. The tibia exhibits a large cnemial crest; though less pronounced than in *A. louisae* (GILMORE, 1936) it is at least twice as long (proximodistally) as *Diplodocus carnegii* (HATCHER, 1901). The distal end of the tibia is also expanded mediolaterally, similar to that seen in *A. louisae* (Fig.13).

The fibulae compare well with *Apatosaurus*, including broad anteroposteriorly expanded proximal and distal ends. The *M. biceps femoris* scar is pronounced, as described for *Apatosaurus* (GILMORE, 1936). This contrasts with the weakly expanded proximal and distal ends of the tibia of both *Barosaurus* (McINTOSH, 2005) and *Diplodocus* (HATCHER, 1901).

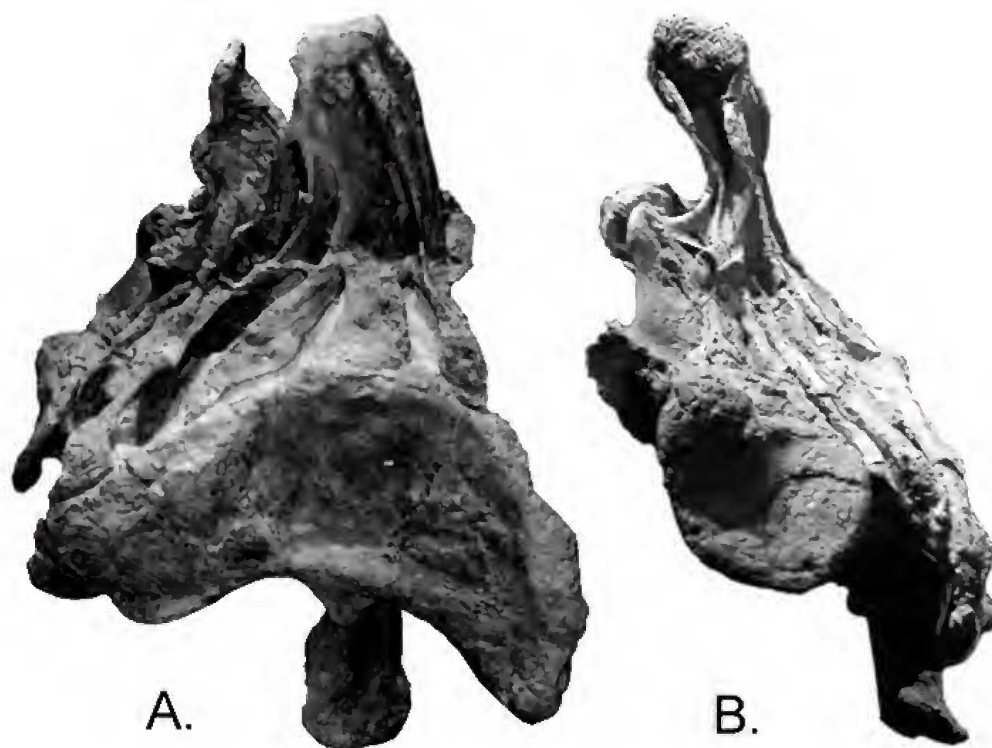


Fig.11- Right lateral (a) and posterior view (b) of *Supersaurus* partial sacrum and articulated right ilium (BYU 13018)s.

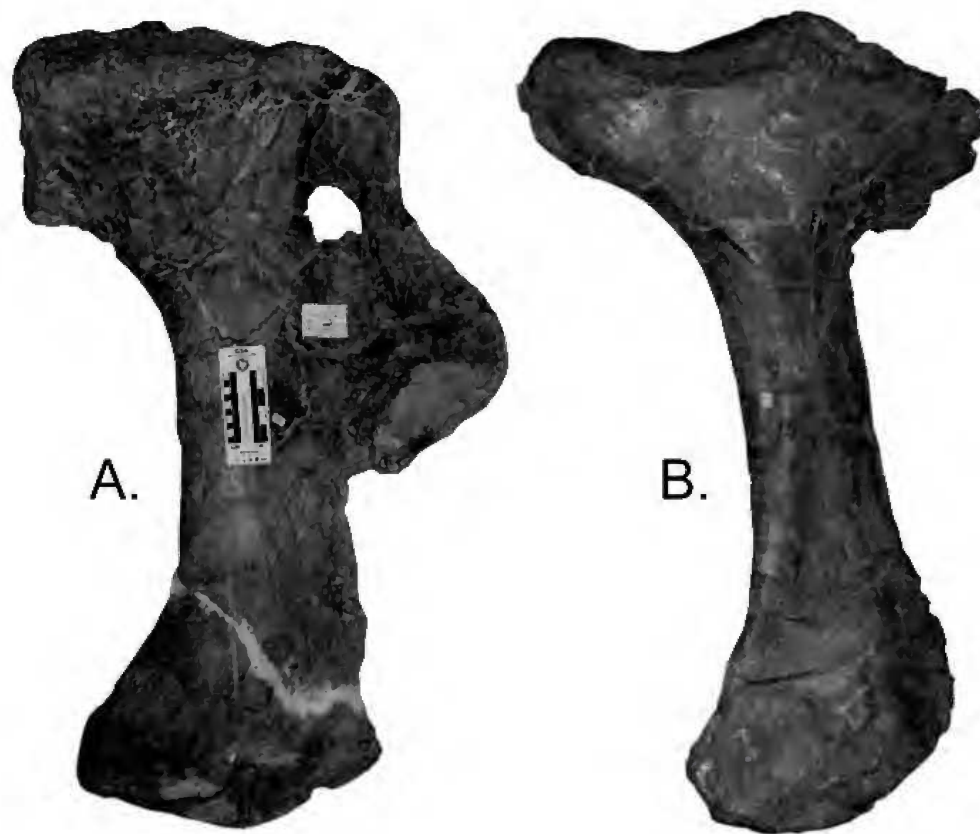


Fig.12- Left lateral view of *Supersaurus* left pubis BYU 12424 (a) and right lateral view of *Supersaurus* right ischium BYU 12946 (b).

PHYLOGENETIC ANALYSIS

The primary phylogenetic analysis (utilizing the modified matrix of HARRIS & DODSON, 2004) resulted in three equally parsimonious trees of 466 steps. The resulting strict consensus tree (Fig.14) has a Confidence Index of 62 and a Retention Index of 78. The analysis recovered a monophyletic Apatosaurinae consisting of *Suuwassea* as the sister taxon to *Apatosaurus* + *Supersaurus*. Inclusion of *Seismosaurus* in the analysis resulted in a sister-group relationship between *Seismosaurus* and *Diplodocus*, with *Barosaurus* as the most basal diplodocine. These results are consistent with the apatosaurine axial morphology of *Suuwassea* (HARRIS, 2006), and corroborates the distinction of *Supersaurus* from *Barosaurus*, *Seismosaurus*, and *Diplodocus*.

It is possible that some similarities between *Supersaurus* and other apatosaurines result from a size-coupled increase in robustness, but it is worth noting that apatosaurine robustness does not correlate with size, and large diplodocines like *Seismosaurus* do not exhibit markedly more robust pelvic or costal elements, making it unlikely that size

is obscuring the phylogenetic signal. Other characters such as proximal centra that are heart-shaped in cross-section, and paired ventral pneumatopores in the cervical vertebrae are certainly decoupled from size. Scoring *Supersaurus* into other published analyses (e.g. UPCHURCH *et al.*, 2004) also recovers a monophyletic Apatosaurinae with *Supersaurus* embedded in it (LOVELACE *et al.*, 2005).

Recovery of *Supersaurus* and *Suuwassea* as non-diplodocine diplodocids demonstrates greater apatosaurine diversity than previously suspected. Apatosaurines have not been reported outside of North America, raising the biogeographic possibility that apatosaurines may have been restricted to North America.

DISCUSSION OF *SEISMOSAURUS* VALIDITY

While *Seismosaurus* was recovered as the sister taxa to *Diplodocus*, it was identical to the scoring of *Diplodocus* prior to the addition of our Character 1 (Appendix 1). It has since been discovered that the hook-shaped distal expansion on the ischia of *Seismosaurus* does not exist (LUCAS *et al.*, 2006),

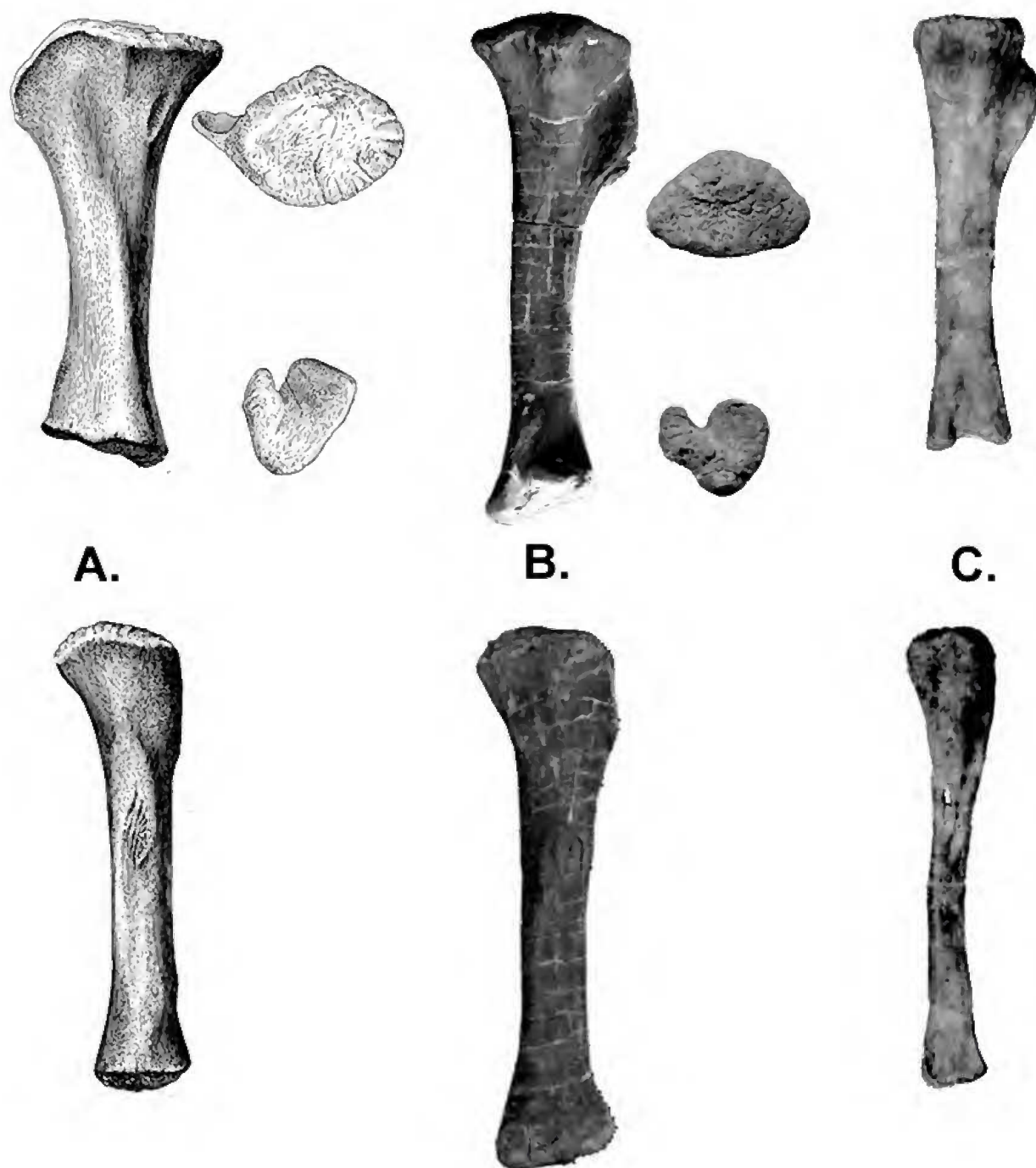


Fig.13- Comparison of tibiae (upper row) and fibulae (lower row) of: A) *Apatosaurus louisae* (GILMORE, 1936), B) *Supersaurus vivianae* (WDC DMJ-021), and C) *Barosaurus lentus* (McINTOSH, 2005).

so *Seismosaurus* is once again indistinguishable from *Diplodocus* in our analysis.

Examining descriptive osteology for *Diplodocus* (OSBORN, 1899; HATCHER, 1901; HOLLAND, 1906; GILMORE, 1932; McINTOSH & CARPENTER, 1998), we concur with CURTICE's (1996) suggestion that the caudal vertebrae of the type of *Seismosaurus* (NMMNH 3690) constitute a nearly continuous series, instead of consisting of

major gaps as suggested by GILLETTE (1991). Following GILLETTE's (1991) numbering of the caudals would require morphology not seen in any diplodocid, including extremely elongate mid-caudal vertebrae with hyper-developed mid-caudal neural spines, and a continuation of the transverse processes far past caudal vertebrae 15-18, the termination point in all other diplodocid taxa (McINTOSH, 2005).

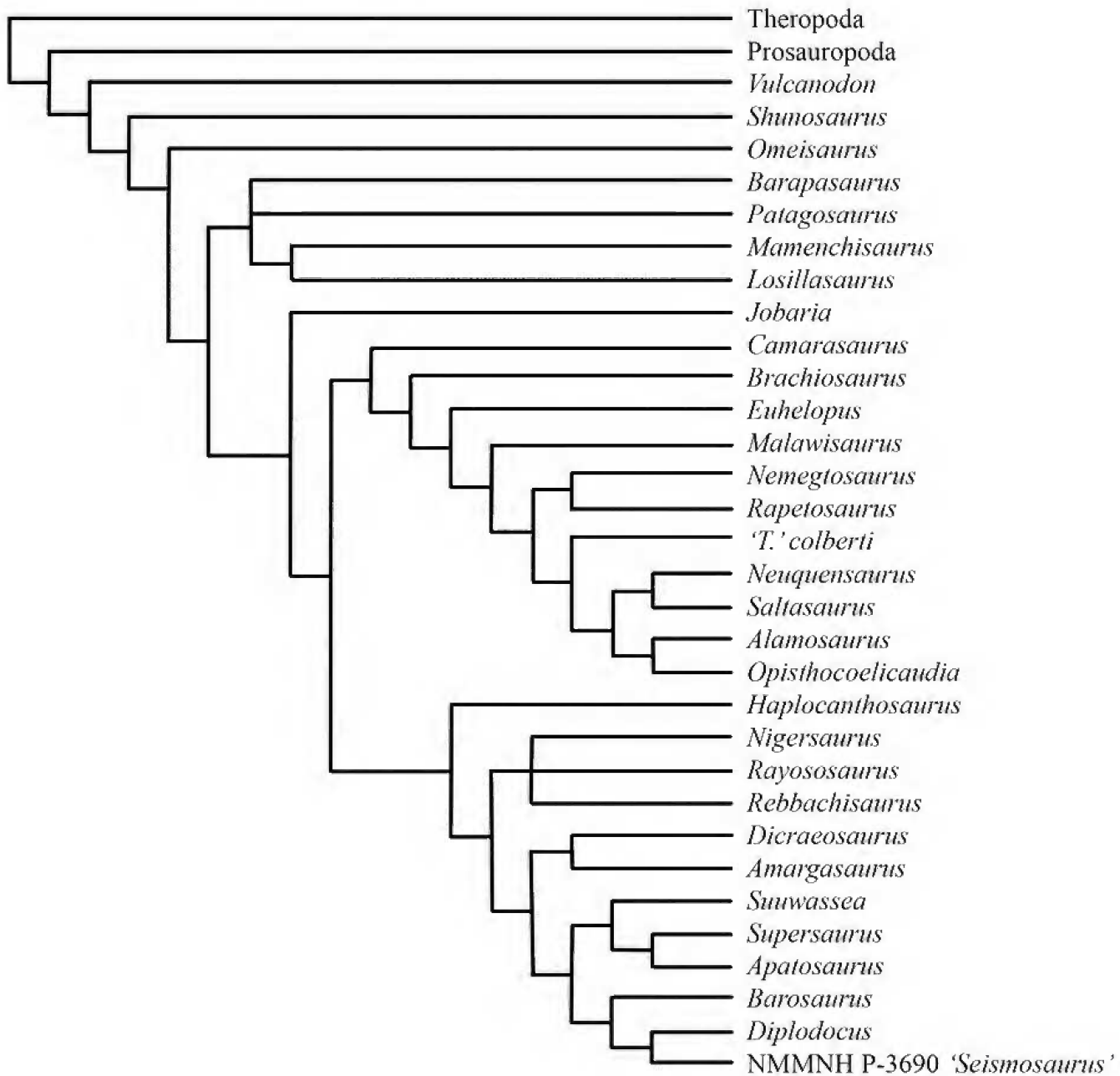


Fig.14- Strict consensus tree resulting from the addition of *Supersaurus* and "*Seismosaurus*" into a modified matrix from HARRIS & DODSON (2004).

Interpreting the caudal series of *Seismosaurus* as a single series of the 22 anterior-most caudals (with perhaps one missing), the morphology is consistent with other diplodocines, and is nearly identical with that described for *Diplodocus longus* (e.g. OSBORN, 1899). The maximum centra length reported by GILLETTE (1991) is 350mm. When compared to the largest caudal vertebrae of *Diplodocus longus* (325mm; GILMORE, 1932) there is only a 2.5cm difference (under 10%).

The remaining caudals are within the range of mid-caudal vertebral lengths reported for *Diplodocus longus* by GILMORE (1932).

The phylogenetic placement of *Seismosaurus* reinforces the osteological finding that *Supersaurus* is distinct from *Seismosaurus*. Based on the extremely similar morphology of the *Seismosaurus* axial and pelvic morphology to specimens of *Diplodocus*, we refer NMMNH 3690 to *Diplodocus*, and most likely to *D. longus*.

SIZE OF THE LARGEST DIPLODOCIDS

While length and mass estimates of extinct animals have utility for constructing paleo-ecological models, there can be little doubt that public fascination is in part responsible for the numerous size estimates in the scientific literature (COLBERT, 1962; GILLETTE, 1991, 1994; PAUL, 1997). Widely varying estimates suggest that more rigor (or perhaps restraint) needs to be applied.

Between the WDC and BYU specimens of *Supersaurus*, most of the presacral axial column is known, and the caudal series is well represented. Using apatosaurine proportions to fill in the missing caudal elements, we reconstruct a length of 33-34m along the axial column for the known specimens of *Supersaurus* (Fig.7), with the BYU specimen being marginally larger.

In comparison, using the proportions of *Diplodocus longus*, we estimate a length of 30m for the NMMNH "seismosaur" specimen (Fig.8). While within the low end of the size estimate provided by D. Gillette (28-36m, 1991), it is far less than the 39-52m length considered "more probable" at the time.

The literature is littered with attempts to estimate the mass of the largest dinosaurs (COLBERT, 1962; ANDERSON, 1989; GILLETTE, 1994; PAUL, 1997). While many studies have used long-bone circumference to estimate mass, we agree with ANDERSON (1989) and PAUL (1997) that variation in the strength index of the femora of extant tetrapods is too great to produce anything more than general ranges. For greater precision we worked with a paleo-life artist to

construct a sculpted model based on the proportions of *Supersaurus* for volumetric measurement (Fig.15). Water-displacement measurements were compared against a 3D laser scan of the model to ensure accuracy of measurement. Assuming a specific gravity of 0.8 (WEDEL, 2004) provides an estimate 35-40 tons in life.

While the more gracile *Seismosaurus* likely massed significantly less, other sauropods such as *Argentinosaurus* clearly achieved much greater bulk.

CONCLUSIONS

WDC DMJ-021 is the second and most complete specimen of *Supersaurus* to date. Because only a single individual was found in the quarry, it serves as a test against elements referred to the type individual found in the Dry Mesa quarry.

With the additional information provided by WDC DMJ-021, enough morphological differences exist to distinguish *Supersaurus* from other diplodocids. Previously ascribed similarities to *Barosaurus* or "*Seismosaurus*" are based upon material inaccurately referred to *Supersaurus*, or to gross similarities in neck elongation or overall size.

Adding *Supersaurus* to existing phylogenetic analyses recovers a more diverse Apatosaurinae than previously thought. Both *Suuwassea* and *Supersaurus* are found to be more closely related to *Apatosaurus* than to other sauropods. At this point apatosaurines appear to be an indigenous clade of North American diplodocid sauropods.

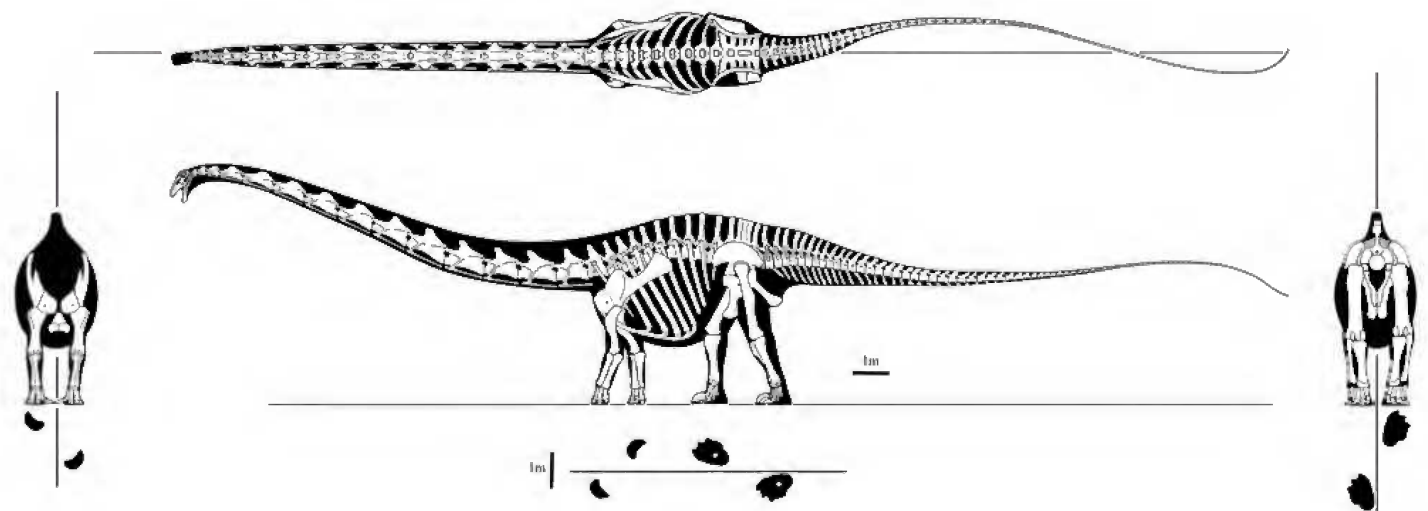


Fig.15- Multiple view skeletal reconstruction used to guide the construction of a physical model for volumetric measurements used in mass estimate.

Greater resolution of diplodocid phylogenetics will likely require a reassessment of individual species of *Apatosaurus* and *Diplodocus*. '*Seismosaurus*' can be referred to the latter, specifically to *D. longus*.

Supersaurus was neither the heaviest nor the longest sauropod, although it is well enough known to place confidence in its estimated length of 33-34 meters, and mass of 35-40 tons.

ACKNOWLEDGMENTS

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APPENDIX 1

SCORING OF *SUPERSAURUS* AND *SEISMOSAURUS*, PLUS ADDITIONAL CHARACTERS (SEE DESCRIPTION IN APPENDIX 2) ADDED INTO THE MATRIX OF HARRIS & DODSON (2004) IN THE PHYLOGENETIC ANALYSIS.

Supersaurus:

??11??0110111111?1
01111111100000021111001100101111011111000001??1110110010110011000??????1011?????????
???????111001101000???????0101110????????????????????????????000000

Seismosaurus:

??11?10
11111111000000211110011011111101111111001????0011001????????????????????????????????
?????110?????1?00??01111

	235	236	237	238		235	236	237	238
Prosauropoda	?	?	?	?	<i>Jobaria</i>	?	?	?	?
Theropoda	?	?	?	?	<i>Malawisaurus</i>	?	?	?	?
<i>Vulcanodon</i>	?	?	?	?	<i>Nigersaurus</i>	?	?	?	?
<i>Barapasaurus</i>	?	?	?	?	<i>Rayososaurus</i>	?	?	?	?
<i>Omeisaurus</i>	?	?	?	?	<i>Rebbachisaurus</i>	?	?	?	?
<i>Shunosaurus</i>	?	?	?	?	<i>Alamosaurus</i>	?	?	?	?
<i>Patagosaurus</i>	?	?	?	?	<i>Nemegtosaurus</i>	?	?	?	?
<i>Mamenchisaurus</i>	?	?	?	?	<i>Neuquensaurus</i>	?	?	?	?
<i>Apatosaurus</i>	0	0	0	0	<i>Opisthocoelicaudia</i>	?	?	?	?
<i>Barosaurus</i>	0	1	0	1	<i>Rapetosaurus</i>	?	?	?	?
<i>Brachiosaurus</i>	?	?	?	?	<i>Saltasaurus</i>	?	?	?	?
<i>Camarasaurus</i>	?	?	?	?	<i>'T.' colberti</i>	?	?	?	?
<i>Dicraeosaurus</i>	0	1	0	0	<i>Supersaurus</i>	0	0	0	0
<i>Diplodocus</i>	0	1	1	1	<i>Suuwassea</i>	?	?	?	?
<i>Haplocanthosaurus</i>	?	?	?	?	<i>Seismosaurus</i>	1	1	1	1
<i>Amargasaurus</i>	?	?	?	?	<i>Losillasaurus</i>	?	?	?	?
<i>Euhelopus</i>	?	?	?	?					

APPENDIX 2

DESCRIPTION OF CHARACTERS ADDED TO HARRIS & DODSON (2004) FOR OUR ANALYSIS.

#235. Posteriorodorsal expansion of distal ischium: absent (0); present (1). This character was needed to separate *Seismosaurus* from *Diplodocus*, otherwise they are scored the same. It has been suggested that might in fact be either a new species of *Diplodocus*, or larger specimen of *D. longus* (Fig.12).

#236. Ratio of neural spine height to centrum height (first caudal vertebrae): less than 2 (0); greater than 2 (1). The height of the neural spine is measured from the top of the centrum to the top of the neural spine. The neural spines of both *Apatosaurus* and *Supersaurus* are relatively shorter than those seen in *Dicraeosaurus*, *Barosaurus*, and *Diplodocus* (Fig.6).

#237. Anterior caudal neural spines bifid: absent (0); present (1). Bifid neural spines are present in the apex of the neural spines in *Diplodocus* and *Seismosaurus*. *Supersaurus* exhibits a wide rectangular distal neural spine (Fig.6).

#238. Location of hyposphene on posterior dorsal vertebrae: less than one half total height of vertebra (0); greater or equal to one half total height of vertebra. The neural arches of the diplodocines are taller than in either *Supersaurus* or *Apatosaurus*, making the neural spines relatively shorter in the diplodocines (Fig.5).